Effect of Disturbance on Assemblages: an Example Using Porifera

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Abstract. Extensive sponge assemblages are found in a number of habitats at Lough Hyne Marine Nature Reserve. These habitats are unusual in experiencing a range of environmental conditions, even though they are only separated by small geographic distances (1–500 m), reducing the possibility of confounding effects between study sites (*e.g.,* silica concentrations and temperature). Sponge assemblages were examined on ephemeral (rocks), stable (cliffs), and artificial (slate panels) hard substrata from high- and low-energy environments that were used to represent two measures of disturbance (flow rate and habitat stability). Sponge assemblages varied considerably between habitat types such that only 26% (25 species) of species reported were common to both rock and cliff habitats. Seven species (of a total of 96 species) were found in the least-developed assemblages (slate panels) and were common to all habitats. Sponge assemblages on rocks and panels varied little between high- and low-energy environments, whereas assemblages inhabiting cliffs varied considerably. Assemblage composition was visualized using Bray-Curtis similarity analysis and Multi-Dimensional Scaling, which enabled differences and similarities between sponge assemblages to be visualized. Cliffs from high- and low-energy sites had different assemblage compositions compared to large rocks, small rocks, and panels, all of which had similar assemblages irrespective of environmental conditions. Differences in assemblages were partially attributed to sponge morphology (shape), as certain morphologies (*e.g.,* arborescent species) were excluded from 2-D rock habitats. Other mechanisms were also considered responsible for the sponge assemblages associated with different habitats.

Introduction

The development of any community (*e.g.,* mature or young) is controlled by a suite of biological and physical factors that may be closely related and interlinked (Buss and Jackson, 1979). In some marine environments, such as caves, communities (all species) are well developed (mature); in others, such as ice-scoured polar shores, all communities tend to be poorly developed (young). Yet there are other localities that contain communities in various stages of development in proximity to one another. Lough Hyne is such an example, where adjacent communities may experience some similar conditions (*e.g.,* flow rate, temperature, food concentration) but are at different stages of development. For example, rocks in areas with fast currents, where disturbance is high, may have less well-developed communities than rocks in areas experiencing slight current flow, where disturbance is reduced (Maughan and Barnes, 2000a), even though they are separated by less than 300 m. The same may be true for sublittoral cliff habitats where climax community states may be achieved only under certain environmental conditions. In the case of rocks, size may also be important to community development because smaller rocks are more likely to be moved than larger rocks, causing differences in community (all species) and assemblage (component phyla) composition (Barnes *et al.,* 1996). Unstable or highly disturbed (*e.g.,* small rocks) habitats are often colonized by fast-growing, opportunistic, and r-strategic species that are able to quickly take advantage of newly created habitats or space (Lilly *et al.,* 1953; Osman, 1977; Sousa, 1979; Barnes *et al.,* 1996; McCook and Chapman, 1997).

Sponges are an important component of hard-substratum communities throughout most polar (*e.g.,* Dayton, 1978), temperate (*e.g.,* Hiscock *et al.,* 1983; Bell and Barnes, 2000a), and tropical regions (*e.g.,* Alcolado, 1990). There is a wide body of literature that considers the influence of

environmental parameters on the composition of sponge assemblages (*e.g.*, Wilkinson and Cheshire, 1989; Alcolad, 1990; Alvarez *et al.*, 1990; Diaz *et al.*, 1990; Schmahl, 1990; Witman and Sebens, 1990). There are also examples of studies comparing sponge assemblages on large (100–1000 km) spatial scales (Maldonado and Uriz, 1995; Hooper *et al.*, 2002) and on smaller scales (2–20 km) between sponges inhabiting mangrove pools (Rützler *et al.*, 2000). However, comparisons between different habitat types (*e.g.*, between loose rock and cliffs) under fixed environmental conditions or on local scales (hundreds of meters) where confounding effects are reduced are less common.

Studies of sponge assemblages suggest that a number of physical factors control species distributions; these factors include water flow rate (Bell and Barnes, 2000a), sedimentation (Könnecker, 1973), nutrient levels (Storr, 1976), depth (Alvarez *et al.*, 1990; Witman and Sebens, 1990), light (Sarà *et al.*, 1978; Cheshire and Wilkinson, 1991), and habitat availability (Könnecker, 1973; Barthel and Tendal, 1993). Habitats classified within these physical parameters (*e.g.*, fast water flow at a depth of 20 m) often contain many smaller or cryptic habitats with their own predefined physical characteristics. For example, at a site of slight water flow, where sedimentation is high, the amount of sediment falling on inclined, vertical, or overhanging cliff surfaces varies considerably, resulting in different assemblages on each surface type (see Bell and Barnes, 2000b, c). Although not as well studied, biological factors are also known to influence the composition of sponge assemblages (see Paine, 1974; Wulff, 1995, 2000), and predation may also limit the local distribution of sponge species (Dunlap and Pawlik, 1996; Wulff, 2000; Bell, 2001). Rich sponge assemblages on sublittoral cliffs at Lough Hyne have been the focus of recent studies, but abundant and diverse sponge populations also occur on the undersides of loose rocks (Lilly *et al.*, 1953; van Soest and Weinberg, 1980; van Soest *et al.*, 1981). At many sites within Lough Hyne, these two habitats can be separated by less than 1 m, providing the opportunity to investigate differences between sponge assemblages occurring in habitats experiencing different levels of stability, without the confounding effects created by larger spatial scales.

The high overall diversity and richness found on hard substrata within Lough Hyne, coupled with the large range of local habitat stability, results in assemblages at various stages of development existing in proximity. Such environmental characteristics provide opportunities to examine the contribution of certain taxa (in this case sponges) to the overall community. This study investigates assemblages inhabiting three substratum types—artificial panels (the most ephemeral), rocks, and cliffs (the most stable)—which represent a qualitative series in terms of habitat stability (*i.e.*, amount of disturbance). The degree of development of sponge assemblages at different levels of habitat stability can be investigated within a particular environmental re-

gime (*e.g.*, fast flow rates). Also, the use of a common substratum (*i.e.*, panel, rock, and cliff) between sites with different environmental conditions (flow regime) gives a second environmental gradient based on flow-rate-generated disturbance (rather than habitat stability). This study attempts to answer four questions: (1) How do sponge assemblages vary with environmental conditions and habitat stability? (2) How does the composition of sponge assemblages vary with water flow rate compared with different rock sizes; both are surrogate measures of disturbance, so do they have similar consequences? (3) Are there discriminating species for (local) habitats of differing stability and flow rates? (4) Are there consistent similarities or differences in assemblage composition in extremes of flow rate and habitat stability?

Materials and Methods

Study site

Lough Hyne Marine Nature Reserve (Fig. 1) is a small (0.5 km^2) temperate sea lough on the southwest coast of Ireland (51°29'N, 9°18'W). It is characterized by a large number of habitats within a small area (Kitching, 1987). Habitats range from current-swept cliff faces to soft-sediment basins where water currents are slight. The lough is connected to the adjacent Atlantic coast by a shallow and narrow channel (The Rapids). This constriction results in an unusual tidal regime whereby water flows into Lough Hyne for about 4 h and out for 8 h. The squeeze causes fast current velocities (>250 cm s^{-1}) in the eastern parts of the lough during inflow, but only slight surface currents in the vicinity of the rapids during outflow (Bassindale *et al.*, 1957). As water moves from east to west across the lough, there is a quick reduction in current flow rate with a corresponding increase in sedimentation.

The small size of Lough Hyne means that communities are only separated on small spatial scales (hundreds of meters). Nevertheless, these communities are discrete because cliff and rock habitats in different parts of the lough are separated by soft sediments. Sponge assemblages are thus isolated and predictable, rather than occurring along a continuous gradient. Different substratum types (*i.e.*, rocks, cliffs, and panels) within a specific environment were separated by less than several meters and therefore not discrete. Panels were sited at Labhra Cliff and Whirlpool Cliff, and rock habitats were sampled at West Cliff and Whirlpool Cliff (Fig. 1). West Cliff and Labhra Cliff have similar sedimentation and rates of water flow, and the sponge assemblages are also similar. Both sites are characterized by slight current flow rates (<5 cm s^{-1}) and heavy sediment accumulation, which increases with depth. Hard substratum extends more than 30 m at both of these sites. Rocks were not sufficiently abundant at Labhra Cliff to sample. Whirlpool Cliff experiences a very fast (>200 cm s^{-1}), unidirectional flow regime, resulting in high disturbance. This site
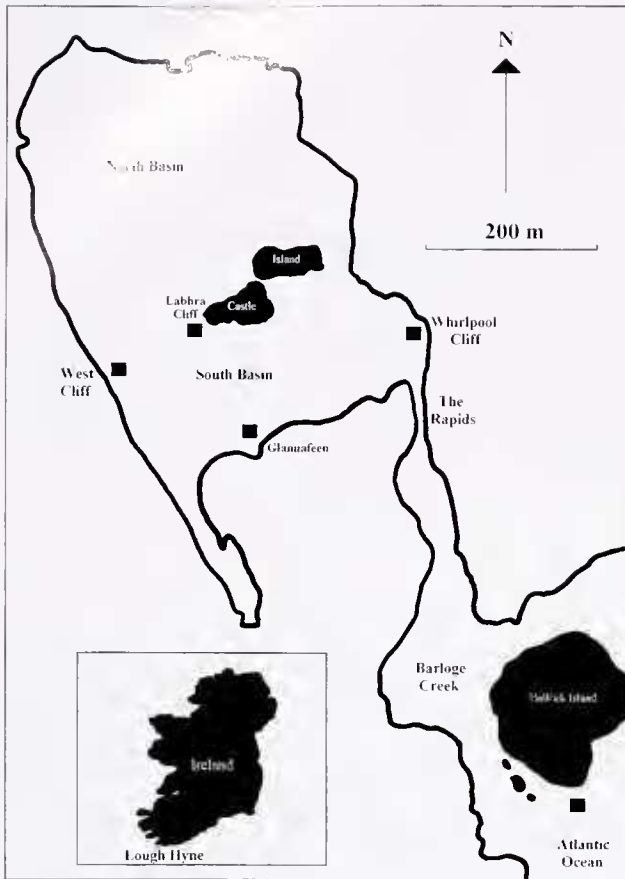
Figure 1.   Sites where sponge rock and cliff assemblages were sampled in Lough Hyne Marine Nature Reserve.

extends to about 18 m, and current flow rates decrease with depth, falling to 100 cm s^{-1} at 18 m (Fig. 2). Some data were taken from the literature (Bell and Barnes, 2000a) to enable greater comparison between sponge assemblages from different habitats within Lough Hyne. These data, which were included in the analysis, concerned sponge assemblages inhabiting vertical and inclined surfaces on sublittoral cliffs at Labhra Cliff, West Cliff, Whirlpool Cliff, and Bullock Island (an adjacent Atlantic coastal site with a turbulent flow regime). The tidal range within Lough Hyne is about 1.5 m.

Sampling and observation methods

The artificial substrata (panels) used were square machined slate panels (15 × 15 cm), prepared and assembled as for Turner and Todd (1994). They were used to investigate an early pioneer stage in community succession. A blue square (10 cm × 10 cm) was drawn in the center of each panel with a permanent blue marker pen. Panels were placed in running water for 24 h and then dried; this process was repeated twice more prior to deployment. The blue background makes it easier to identify recruits that are small or

translucent. Three panels (forming one panel array) were attached by cable ties to welded steel bars. The panel array was positioned with the blue surfaces facing down (to simulate the undersides of a boulder). Bolts at the corner of each steel frame allowed the panels to be adjusted so they were 20 mm above the substratum. Panel arrays were deployed at depths of 0 m, 6 m, and 12 m at Labhra Cliff and Whirlpool Cliff. The first panels were deployed at the start of October 1997 and were replaced bimonthly until March 2001. Before panels were replaced, they were cleaned using a razor blade. Each panel was examined under a binocular microscope, and the number of sponge recruits was recorded. Spicule preparations of sponge recruits were made to confirm identification. Additional panel arrays were placed at the same depths, but were not replaced bimonthly. Each panel was photographed 1, 2, 6, and 12 months after the date of deployment. Photographs were then projected onto a grid composed of 400 random dots, and the percentage cover of sponges on each panel was estimated. The mean percent cover was calculated for panels submerged at each time interval.

Twenty-five rocks were randomly selected within three size classes—small (10–150 cm^2), medium (151–500 cm^2), large (501–1000 cm s^{-1}), and very large (1001–2000 cm s^{-1}) such that equal numbers of boulders of each size were examined (*i.e.*, this does not represent the true boulder size distribution). The surface areas of both upper and lower rock surfaces were measured using a transparent cloth marked in square centimeters. The number of sponges (number of patches) for each species on each rock was recorded. Each species was photographed, and samples were taken for spicule analysis to confirm identification. Sponge samples were dissolved in concentrated nitric acid, or bleach as required, and were examined through a compound microscope at high power (×400). All observations were made between October 1999 and February 2000, which eliminated faunistic inter-site differences caused by seasonal growth or tissue retraction over the study period.

The morphologies of all sponges observed on rocks were classified within the following groups (after Boury-Esnault and Rüizler, 1997; Bell and Barnes, 2000d): encrusting (EN), flabellate (FL), clathrate (CL), massive (MA), arborescent (AR), repent (RE), tubular (TU), ficiform (FI), massive globulose (MG), and papillate (PA).

Data visualization and statistical procedures

Data were subjected to Bray-Curtis similarity analysis using hierarchical agglomerative group-average clustering for all habitats and depths (including data from Bell and Barnes, 2000a). This analysis was performed using the unweighted pair group method using arithmetic averages (UPGMA) with the PRIMER program (ver. 5.2.8, Plymouth Marine Laboratory, Plymouth, England). Data were log (x + 1) transformed to reduce the importance of extreme
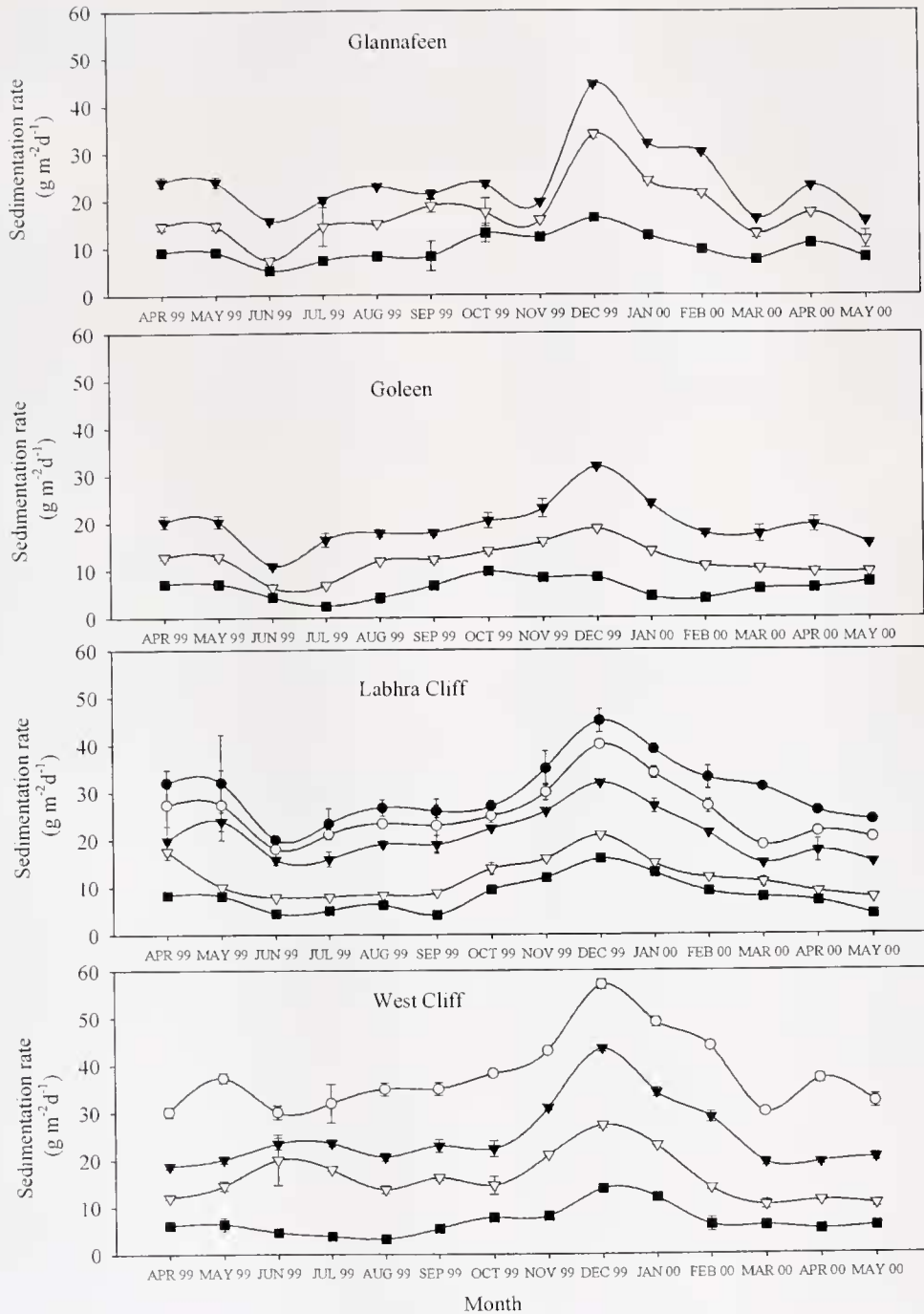
Figure 2. Annual variation in sedimentation rates (g sediment m^{-2}d^{-1}) at 6-m depth intervals at four sublittoral cliff sites within Lough Hyne. 6 m (■) 12 m (□) 18 m (▼) 24 m (○) 30 m (●). Standard error bars are shown. [After Bell (2001).]

values (rare species). Ordination by non-metric Multi-Dimensional Scaling (MDS in PRIMER) was undertaken on a dissimilarity matrix created from Bray-Curtis similarity analysis. SIMPER analysis (in PRIMER) was used to determine the contribution of each species to the average Bray-Curtis dissimilarity between habitats and sites. This method of analysis determines which species are responsi-

ble for any differences that occur. Data were transformed as for Bray-Curtis analysis. Because sampling areas differed between habitat types, the area of each habitat and the abundance of each species were scaled up or down to standardize sampling areas between sites, depths, and habitats (sponges m^{-2}).

Patterns of species diversity for sponge assemblages on

rocks were described with the Shannon and Weiner (Krebs, 1989) information function $H' = -\Sigma p_i ln \ p_i$. Paired Student's t tests were used to examine differences between rock surface types. A general linear model analysis of variance (GLM ANOVA) was used to compare logarithmically (Log10) transformed sponge species diversity, richness, and rock surface area relationships between West Cliff and Whirlpool Cliff. The same method was used to compare the untransformed relationship between sponge density and rock surface area. This method compares the average linear relationship to an average linear relationship fitted to all the data. Kruskall-Wallis tests were used to compare the differences between percentage cover on submerged panels after 1, 2, 6, and 12 months.

Results

Assemblage composition

A total of 96 species were reported during this study, 44 of which were found on rocks and 76 from cliff habitats (Table 1). Twenty-five sponge species were shared between rock and cliff habitats. All but two of the species (*Hymeniacidon perlevis* and *Halichondria bowerbanki*) of sponge found on rocks occurred on the undersides. These two species were often found growing on the fronds of algae as well as on rock surfaces. Although sponge assemblages varied considerably between habitat types, there was little variation between rock sponge assemblages inhabiting the different sites (extremes of water flow rate) (Table 2). Of the 44 species inhabiting rocks, only 7 (16%) differed between West Cliff and Whirlpool Cliff, with only 1 of these species (*Mycale rotalis*) being found exclusively at Whirlpool Cliff. The remaining 6 species were only found at West Cliff. Nineteen of the 44 species found on rocks were exclusive to rock habitats, illustrating the high degree of species exclusivity within this habitat type. The panels at Labhra Cliff and Whirlpool Cliff showed no exclusive species, and only 7 species of sponge were reported (Table 1). Therefore, no juvenile settlement was recorded for the majority of sponge species reported during this study despite the nearly 4-year duration of panel deployment. All species found on panels occurred in both rock and cliff habitats. Because panels can be considered a similar habitat to rocks (but younger in terms of community development), community age was the most likely determinant of the composition of the sponge assemblage. Of the total 76 species of sponge reported from cliff habitats, 31 species (data included from Bell and Barnes, 2000a) were found at Bullock Island, compared to 40 species at Whirlpool Cliff and 52 from both Labhra Cliff and West Cliff (Table 3). Although many of these species were shared between cliff habitats, only 10 of the total 76 species were shared between all cliff habitats. Environmental parameters, therefore, proved important in determining the sponge assemblage in cliff habitats. A much higher proportion of species were shared within the same habitat

than between different habitat types (Table 3). However, the proportion of species shared between sites was higher for rock and panel habitats (>85%) than for cliff habitats (<50%).

Sponge morphology

On rocks, encrusting morphologies were the most abundant form (20 of 44 species), followed by massive (15 of 44 species) and repent forms (7 of 44 species) (all pooled rock data). The remaining species exhibited cylindrical (*Scypha ciliatum*) and clathrate forms (*Clathrina coriacea*). On cliff surfaces, 30 species were encrusting, 19 were massive, and 6 exhibited repent forms (pooling cliff data). Sponge species on panels had a wide range of morphologies (given the small number of species), including tubular, repent, encrusting, massive, and clathrate forms. Differences were observed between the proportions of sponge morphologies between certain habitats and sites (Table 4). There was a considerable difference between the proportion of morphologies between cliff sites (Table 3). Encrusting forms were more abundant at the high-energy cliff sites (Bullock Island and Whirlpool Cliff) than at low-energy sites (Labhra Cliff and West Cliff), where they were replaced by arborescent and papillate forms. In rock habitats, high proportions of encrusting and massive forms were found, with no differences between sites. Panel assemblages were also very similar in the proportions of morphologies between sites.

Identification of different sponge assemblages

Small sponges were difficult to identify, (particularly on panels) and potentially represent an error in the analysis. However, this problem was reduced by the transformation of the data prior to analysis, which decreased the importance of extreme values or apparent rare species.

Bray-Curtis similarity analysis and Multi-Dimensional Scaling (MDS) (Fig. 4) were used to distinguish between sponge assemblages within different habitats and sites. The Bray-Curtis analysis identified five major assemblage groups that showed increasing similarity, as follows: rocks (all sites and sizes), panels (all sites), Whirlpool Cliff, Bullock Island, and Labhra Cliff/West Cliff. However, each major assemblage group had a very low similarity (<25%) with the others. MDS distinguished two additional, smaller assemblages, which were not obvious from the Bray-Curtis analysis. The first of these assemblages was at 30 m at Labhra Cliff; it showed the greatest affinity with the other cluster at Labhra Cliff and West Cliff (cliff habitat). The second assemblage was composed of 0-m sponges at Labhra Cliff and West Cliff (cliff habitat). These assemblages were most similar to those at Whirlpool Cliff. The subtidal (6 and 12 m) panels had high levels of correspondence (≈65%) between sites, but differed considerably from those in the intertidal zone (0 m) (≈30% similarity). To account for morphological differences created by the nature of the dif-

Table 1

Sponge species found within Lough Hyne on sublittoral cliff and rocks and on the adjacent Atlantic coast

	BU	WH	LA	WC		BU	WH	LA	WC
Antho involvens (EN)	*			*	*Hymeraphia stellifera* (EN)	*	*	*	*
Antho inconstans # (EN)					*Iophon hyndmani* (EN)		*		
Aplysilla rosea (EN)			*	*	*Iophon ingalli* (EN)	*	*		
Aplysilla sulfurea (EN)	*	*	*	*	*Iophonopsis nigricans* (EN)	*			
Axinella damicornis (FL)			*	*	*Laxosuberites incrustans* (EN)		*		
Axinella dissimilis (AR)		*	*	*	**Leucosolenia complicata** (RE)	*	*		
Biemna variantia (MA)			*	*	*Leuconia nivea* (EN)	*	*		
Clathrina coriacea (CL)		*	*	*	*Microciona fallax* # (EN)				
Cliona celata (MA)	*	*	*	*	*Microciona strepsitoxa* # (EN)				
Dercitus bucklandi # (MA)					*Mycale contarenii* (MA)		*	*	*
Dysidea fragilis (MA)	*	*	*	*	*Mycale macilenta* (MA)				*
Dysidea pallescens (MA)			*	*	*Mycale rotalis* (MA)		*		*
Esperiopsis fucorum (RE)	*	*			*Myxilla rosacea* (EN)	*			*
Eurypon sp. 1 (EN)			*	*	*Myxilla incrustans* (EN)				
Eurypon sp. 2 (EN)			*	*	*Myxilla fimbriata* (MA)		*		
Eurypon sp. 3 (EN)			*	*	*Pachymatisma johnstonia* (MA)	*	*		
Eurypon sp. 4 (EN)			*	*	*Parotimea constellata* (EN)	*	*	*	*
Eurypon sp. 5 (EN)			*	*	*Phakellia* sp. (PA)			*	*
Eurypon sp. 6 (EN)			*	*	*Phorbas fictitius* (EN)	*	*		
Eurypon sp. 7 (EN)			*	*	*Plakortis simplex* (EN)		*	*	
Eurypon sp. 8 (EN)			*	*	*Plocamilla coriacea* # (EN)				
Halichondria bowerbanki (RE)		*	*	*	*Polymastia* sp. 1 (PA)			*	*
Halichondria panicea (EN)	*	*			*Polymastia* sp. 2 (PA)			*	*
Haliclona cinerea (MA)		*			*Polymastia* sp. 3 (PA)			*	*
Haliclona fistulosa (RE)	*	*	*	*	*Polymastia* sp. 4 (PA)	*		*	*
Haliclona simulans (RE)		*			*Polymastia* sp. 5 (PA)	*		*	*
Haliclona sp. 1 (MA)	*		*	*	*Polymastia* sp. 6 (PA)			*	*
Haliclona sp. 2 (MA)	*		*	*	*Polymastia* sp. 7 (PA)		*	*	*
Haliclona sp. 3 (RE)	*				*Polymastia* sp. 8 (PA)		*	*	*
Haliclona sp. 4 (MA)		*	*	*	*Pseudosuberites sulphureus* (EN)	*	*		
Haliclona sp. 5 (MA)	*	*			*Rhaphidostyla kitchingi* (AR)	*	*		
Haliclona sp. 6 # (MA)					*Raspailia hispida* (AR)		*	*	*
Haliclona sp. 7 # (RE)					*Raspailia ramosa* (AR)		*	*	*
Haliclona sp. 8 # (RE)					**Scypha cilatum** (TU)	*	*	*	*
Haliclona sp. 9 # (RE)					*Spanioplon armaturum* # (EN)				
Haliclona sp. 10 # (MA)					*Stelligera rigida* (FL)		*	*	*
Haliclona sp. 11 # (MA)					*Stelligera stuposa* (AR)*	*	*	*	
Haliclona sp. 12 # (RE)					*Stylostichon dives* (EN)		*		
Haliclona urceolus (TU)			*	*	*Stylostichon plumosum* # (MA)				
Haliclona viscosa (MA)			*		*Suberites carnosus* (FI)			*	*
Halicnemia patera (EN)			*	*	*Suberites ficus* (FI)			*	*
Halisarca sp. (MA)			*		*Suberites* sp. 1 (EN)			*	*
Hemimycale columella (EN)	*	*			*Suberites* sp. 2 (EN)	*	*	*	
Hymedesmia brondstedi # (EN)					*Suberites* sp. 3 (EN)	*	*		
Hymedesmia jecusculum # (EN)					*Suberites* sp. 4 (EN)	*			
Hymedesmia pansa # (EN)					*Terpias fugax* # (EN)				
Hymedesmia paupertus (EN)			*	*	*Tethya auranaum* (MG)	*	*	*	*
Hymeniacidon perlevis (MA)	*	*	*	*	**Unidentified sponges**				

An asterisk indicates species found at a particular site (BU, Bullock Island; WH, Whirlpool Cliff; LA. Labhra Cliff; WC, West Cliff). Underlining denotes species found on rocks, and the symbol # indicates that the species was exclusive to rocks; boldface type denotes species found on panels (none were exclusive). Uppercase letters in parentheses after the species name are macro-morphological descriptions: AR, arborescent; CL, clathrate; EN, encrusting; FI, ficiform; FL, flabellate; MA, massive; MG, massive globulose; PA, papillate; RE, repent; TU, tubular.

ferent habitats, the same MDS and Bray-Curtis analysis was repeated using only species that exhibited encrusting or massive morphologies. However, no differences were ob-

served between the original dendrogram and the 2-D scaling plot produced (output not shown).

SIMPER analysis was used to determine which species

Table 2

Sponge species that were reported from the under (*) and upper (+) sides of rocks found at two sites at Lough Hyne

Species (Morphology)#	West Cliff†				Whirlpool Cliff†			
	S	M	L	VL	S	M	L	VL
Antho inconstans (EN)			*	*	*	*	*	*
Antho involvens (EN)			*	*			*	*
Aplysilla sulfurea (EN)	*	*	*	*	*	*	*	*
Aplysilla rosea (EN)	*	*	*	*	*	*	*	*
Clathrina coriacea (CL)	*	*	*	*	*	*	*	*
Cliona celata (MA)			*	*			*	*
Dercitus bucklandi (MA)		*	*	*		*	*	*
Dysidea fragilis (MA)	*	*	*	*	*	*	*	*
Dysidea pallescens (MA)			*	*			*	*
Esperiopsis fucorum (RE)		*	*	*		*	*	*
Haliclona sp. 1 (MA)	*	*	*	*			*	*
Haliclona sp. 2 (RE)	*	*	*	*	*	*	*	*
Haliclona sp. 3 (RE)		*	*	*	*	*	*	*
Haliclona sp. 4 (RE)	*	*	*	*	*	*	*	*
Haliclona sp. 5 (MA)	*	*	*	*	*	*	*	*
Haliclona sp. 6 (MA)	*	*	*	*	*	*	*	*
Haliclona sp. 7 (MA)		*	*	*		*	*	*
Haliclona sp. 8 (MA)	*	*	*	*		*	*	*
Halichondria bowerbanki (RE)+			*+	*+			*+	*+
Hymedesmia brondstedi (EN)	*	*	*	*	*	*	*	*
Hymedesmia jecusculum? (EN)				*			*	*
Hymedesmia pansa (EN)				*		*	*	*
Hymedesmia paupertas (EN)		*	*	*		*	*	*
Hymeniacidon perlevis (MA)+	*+	*+	*+	*+	*+	*+	*+	*+
Iophon ingalli (EN)				*				*
Leuconia nivea (EN)		*	*	*				
Leucosolenia complicata (RE)	*	*	*	*	*	*	*	*
Microciona fallax (EN)		*	*	*				
Microciona strepsitoxa (EN)				*			*	*
Mycale contarenii (MA)			*	*				
Mycale macilenta (MA)			*	*				
Mycale rotalis (MA)							*	*
Myxilla rosacea (MA)	*	*	*			*	*	*
Myxilla incrustans (EN)				*				
Pachymatisma johnstonia (MA)		*	*	*	*	*	*	*
Phorbas fictitius (EN)			*	*				
Plakortis simplex (EN)	*	*	*	*	*	*	*	*
Plocamilla coriacea? (EN)				*				*
Scypha ciliatum (TU)		*	*	*			*	*
Spanioplon armaturum (EN)			*	*		*	*	*
Stylostichon dives (EN)	*	*	*	*	*	*	*	*
Stylostichon plumosum (MA)	*	*	*	*	*	*	*	*
Suberites sp. (EN)	*	*	*	*		*	*	*
Terpios fugax (EN)			*	*		*	*	*
Total number of species	18	27	37	43	17	25	30	30

The morphological group of each species is given in parentheses: CL, clathrate; EN, encrusting; MA, massive; RE, repent; TU, tubular.

† Four sizes of rock were distinguished: S, small; M, medium; L, large, VL, very large.

were most responsible for the differences seen between sites and habitats with the Bray-Curtis analysis. Only the top five of these indicator, or "discriminating" species (those with the least similarity between different habitats) are illustrated (Table 5). The discriminating species between rock habitats (irrespective of site) and all other habitats were very similar. *Plakortis simplex, Clathrina coriacea, Aplysilla rosacea,*

H. brondstedi, and *L. complicata* can all be considered indicative of rock habitats. When the rock assemblages from West Cliff and Whirlpool Cliff were compared, the discriminating species were, however, not those found at only one of the sites. The most important discriminating species from the cliffs at Bullock Island was *Hemimycale columella.* In most cases, Whirlpool Cliff could be characterized by the

Table 3

The number of sponge species shared between sites

Site	WC (B) (43) ↓	WH (B) (38) ↓	BI (C) (31) ↓	WH (C) (40) ↓	LC (C) (52) ↓	WC (C) (52) ↓	WH (P) (7) ↓
WH (B) (38)	37 (84%)						
BI (C) (31)	14 (23%)	13 (23%)					
WH (C) (40)	16 (23%)	17 (28%)	22 (45%)				
LC (C) (52)	13 (16%)	13 (17%)	15 (22%)	22 (31%)			
WC (C) (52)	15 (19%)	16 (22%)	16 (24%)	20 (28%)	48 (86%)		
WH (P) (7)	6 (14%)	6 (15%)	5 (15%)	6 (15%)	3 (5%)	3 (5%)	
WC (P) (7)	6 (14%)	6 (15%)	5 (15%)	6 (15%)	3 (5%)	3 (5%)	7 (100%)

Numbers in parentheses indicate total number of species at each site and habitat. C, cliff; B, rock; P, panel; WC, West Cliff; WH, Whirlpool Cliff; BI, Bullock Island; LC, Labhra Cliff. % indicates the proportion of all species shared for each pair of habitats: % = number of shared species ÷ (number of species at habitat A × number of species at habitat B) − number of shared species.

presence of *Esperiopsis fucorum* and *Scypha ciliatum*. For panel habitats, it was not possible to identify true discriminating species because only seven species were reported from panels. Therefore, the technique of using individual species as discriminating, or indicator, species was not applicable in these very young (panel) sponge assemblages.

Development of assemblages on panels

The contribution of sponges to early community development (panels) varied considerably between Whirlpool Cliff and Labhra Cliff (Fig. 5). The percentage cover of sponges on subtidal panels at Whirlpool Cliff and Labhra Cliff increased significantly (from about 0% to between 4% and 10% cover) over the 12-month period (Kruskal-Wallis, $H < 11.12$, $P < 0.01$, df = 4). In contrast, sponges did not constitute any part of the community on intertidal panels at either site (irrespective of time interval). At Labhra Cliff, the panels did not have a significantly higher percentage cover of sponges than at Whirlpool Cliff after 1, 2, or 6 months (at either 6 or 12 m). However, a significantly higher percentage cover (twice as high) of sponges was found on panels at Labhra Cliff than at Whirlpool Cliff after 12-month deployments at both 6 and 12 m (Mann-Whitney, $W = 144$, $P < 0.01$, df = 5).

Table 4

The number of sponge species showing different morphological types at different sites and habitats at Lough Hyne and the percentage of each morphology as a proportion of the total number of species

Site*	Morphological Group†									
	EN	MA	RE	PA	FL	CL	AR	TU	FI	MG
Bullock Island (C)	14	8	4	2	0	0	1	1	0	1
	45%	26%	13%	6%	0%	0%	3%	3%	0%	3%
Whirlpool Cliff (C)	16	10	5	2	0	1	4	1	0	1
	40%	25%	13%	5%	0%	3%	10%	3%	0%	3%
Labhra Cliff (C)	17	12	2	9	2	1	5	2	1	1
	33%	23%	4%	17%	4%	2%	10%	4%	2%	2%
West Cliff (C)	16	13	2	9	2	1	5	2	1	1
	31%	25%	4%	17%	4%	2%	10%	4%	2%	2%
Whirlpool Cliff (B)	16	14	6	0	0	1	0	1	0	0
	42%	37%	16%	0%	0%	3%	0%	3%	0%	0%
West Cliff (B)	20	15	6	0	0	1	0	1	0	0
	47%	35%	14%	0%	0%	2%	0%	2%	0%	0%
Whirlpool Cliff (P)	1	1	1	0	0	1	0	1	0	0
	17%	17%	17%	0%	0%	17%	0%	17%	0%	0%
Labhra Cliff (P)	1	1	2	0	0	1	0	1	0	0
	17%	17%	33%	0%	0%	17%	0%	17%	0%	0%

* C, cliff; B, rocks; P, panels.

† EN, encrusting; MA, massive; RE, repent; PA, papillate; FL, flabellate; CL, clathrate; AR, arborescent; TU, tubular; FI, ficiform; MG, massive globulose.
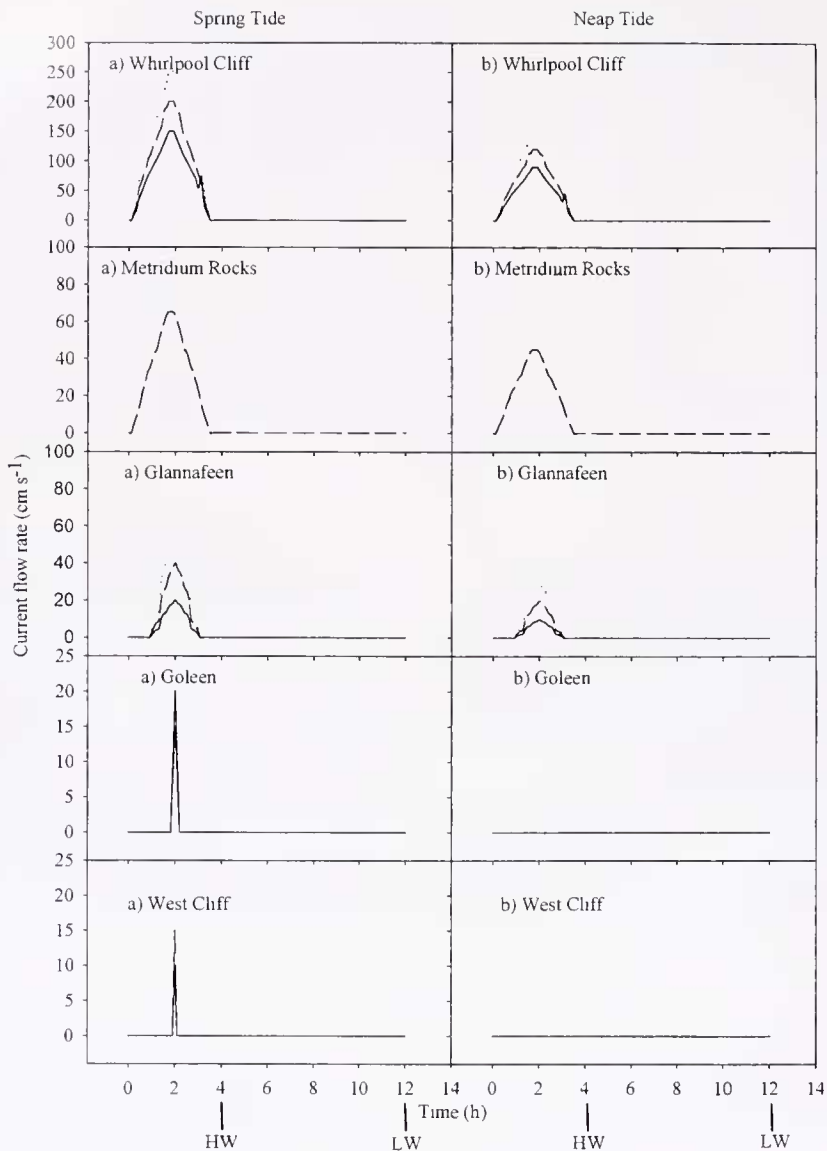
Figure 3. Spring (a) and neap (b) tide flow rates over one tidal period at four sites within Lough Hyne. Note that graphs have different y axes. [After Bell (2001).]

Assemblages on rocks

Bray-Curtis analysis and MDS showed that sponge assemblages on rock had a very high level of similarity (65%) between sites and different rock sizes (Fig. 4). But, when the cluster composed of assemblages from various sized rocks was considered alone, assemblages inhabiting medium, large, and very large rocks had a greater similarity between different sites than the assemblages on small rocks had with other rock sizes within the same site. At both sites, assemblages on medium, large, and very large boulders gave rise to clusters that then formed a larger cluster with the small rock assemblages. Rock size had important influences on sponge assemblages (Table 2). A higher number of species was reported from larger rather than smaller rocks at both

sites (as expected given the area effect). Yet few differences were observed between the sponge assemblages on the small and medium-sized rocks at West Cliff and Labhra Cliff.

There was a logarithmic relationship between substratum area and sponge species diversity on rocks from both West Cliff and Whirlpool Cliff. Data were Log10 transformed, resulting in linear relationships (Fig. 6). The relationship between the number of sponges (per rock) and the area of rock surface at both sites was linear (Fig. 7). General linear model (GLM) ANOVA was used to compare the linear relationships between substratum area, number of sponges, and diversity. In the relationships between species diversity and area, no significant difference was observed in slope or
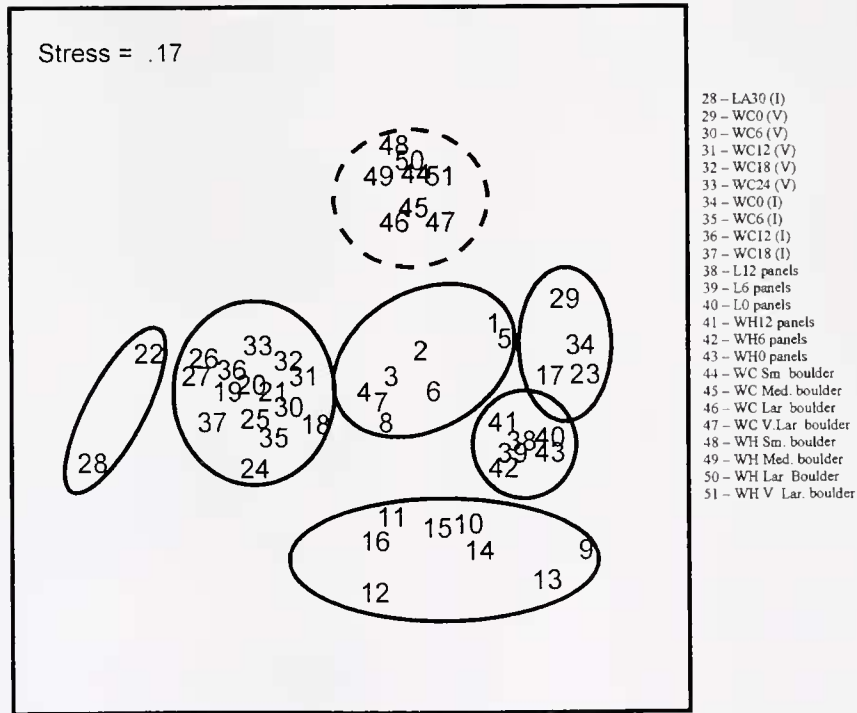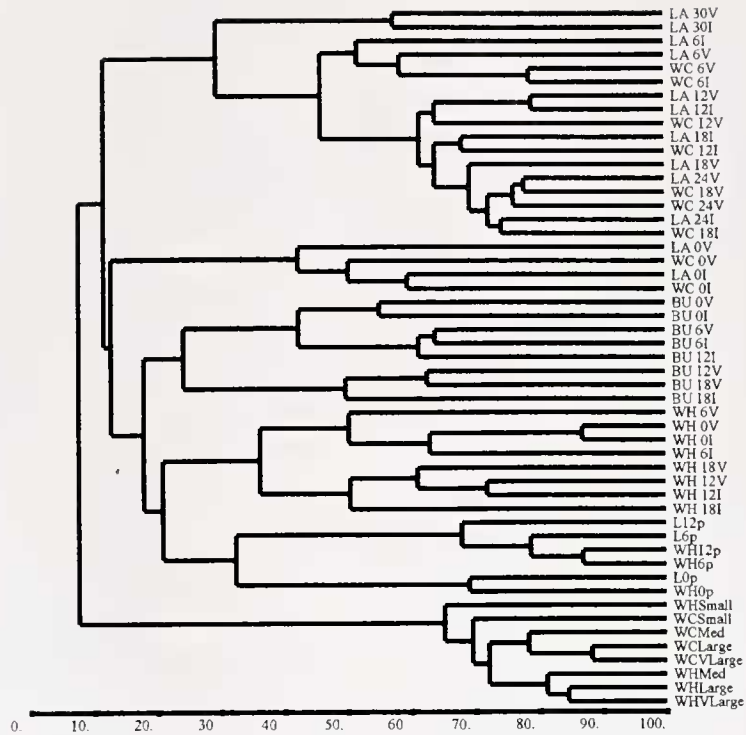
Stress = .17

1 – WH0 (V)
2 – WH6 (V)
3 – WH12 (V)
4 – WH18 (V)
5 – WH0 (I)
6 – WH6 (I)
7 – WH12 (I)
8 – WH18 (I)
9 – BU0 (V)
10 – BU6 (V)
11 – BU12 (V)
12 – BU18 (V)
13 – BU0 (I)
14 – BU6 (I)
15 – BU 12 (I)
16 – BU18 (I)
17 – LA0 (V)
18 – LA6 (V)
19 – LA12 (V)
20 – LA 18 (V)
21 – LA 24 (V)
22 – LA30 (V)
23 – LA0 (I)
24 – LA6 (I)
25 – LA12 (I)
26 – LA18 (I)
27 – LA24 (I)

28 – LA30 (I)
29 – WC0 (V)
30 – WC6 (V)
31 – WC12 (V)
32 – WC18 (V)
33 – WC24 (V)
34 – WC0 (I)
35 – WC6 (I)
36 – WC12 (I)
37 – WC18 (I)
38 – L12 panels
39 – L6 panels
40 – L0 panels
41 – WH12 panels
42 – WH6 panels
43 – WH0 panels
44 – WC Sm. boulder
45 – WC Med. boulder
46 – WC Lar. boulder
47 – WC V.Lar. boulder
48 – WH Sm. boulder
49 – WH Med. boulder
50 – WH Lar. Boulder
51 – WH V Lar. boulder

Figure 4. Bray-Curtis similarity and Multi-Dimensional Scaling (MDS) analysis to compare the sponge assemblages inhabiting panels, rocks, and cliff at a number of sites, depths, and surface inclinations from Lough Hyne. The dashed circle indicates the grouping that MDS produced for loose rock assemblages.

intercept between West Cliff and Whirlpool Cliff (GLM ANOVA; F ratio = 0.07, P = 0.78, denominator df = 1, numerator df = 278). This was also true for the transformed

relationships between species richness and rock surface area at West Cliff and Whirlpool Cliff (graph not shown) (GLM ANOVA; F-ratio = 1.1, P = 0.25, denominator df = 1,

Table 5

Simper analysis (Primer) to determine the five most dissimilar species in terms of percentage abundance for each pair of habitats/sites

Site	West Cliff (cliff) ↓	Whirlpool Cliff (rocks) ↓	West Cliff (rocks) ↓	Whirlpool Cliff (cliff) ↓	Bullock Island (cliff) ↓	Labhra Cliff (panels) ↓	Labhra Cliff (cliff) ↓
Whirlpool Cliff (rocks)	Plakortis simplex*; Clathrina coriacea*; Aplysilla rosacea*; H. brøndstedi*; L. complicata*						
West Cliff (rocks)	Plakortis simplex*; A. rosacea*; Clathrina coriacea*; Haliclona sp. 7*; H. brøndstedi*	Haliclona sp. 6; Hymedesmia pansa; Hymeniacidon perlevis*; Scypha ciliatum*; Leuconia nivea*					
Whirlpool Cliff (cliff)	Esperiopsis fucorum*; Scypha ciliatum*; Suberites carnosus; Eurypon orange; Stelligera rigida	Plakortis simplex; Clathrina coriacea; Aplysilla rosacea; H. brøndstedi; L. complicata	Plakortis simplex; Aplysilla rosacea; Haliclona sp. 7; H. brøndstedi; Clathrina coriacea				
Bullock Island (cliff)	Halichondria panacea*; Suberites carnosus; Stelligera rigida; Raspailia ramosa; Hemimycale columella*	Plakortis simplex; Clathrina coriacea; H. brøndstedi; L. complicata	Plakortis simplex; Aplysilla rosacea; Clathrina coriacea; Haliclona sp. 7; H. brøndstedi	Halichondria panacea*; Suberites carnosus; Stelligera rigida; Raspailia ramosa; Hemimycale columella*			
Labhra Cliff (panels)	Scypha ciliatum*; Stelligera rigida; Suberites carnosus; Raspailia ramosa; Eurypon orange	Plakortis simplex; Clathrina coriacea; Aplysilla rosacea; H. brøndstedi; L. complicata	Plakortis simplex; A. rosacea; Haliclona sp. 7; H. brøndstedi; Clathrina coriacea	Esperiopsis fucorum; Scypha ciliatum; Tethya aurantium; Dysidea fragilis; Haliclona sp. 4	Scypha ciliatum*; Halichondria panacea*; Dysidea fragilis*; Hemimycale columella; Cliona celata		
Labhra Cliff (cliff)	Suberites carnosus*; Haliclona sp. 4*; Eurypon orange; Raspailia ramosa*; Paratinea constellata*	Plakortis simplex; Clathrina coriacea; Aplysilla rosacea; H. brøndstedi; L. complicata	Plakortis simplex; A. rosacea; Clathrina coriacea; Haliclona sp. 7; H. brøndstedi	Esperiopsis fucorum; Scypha ciliatum; Haliclona sp. 4; Eurypon major*; Stelligera rigida*	Halichondria panacea; Stelligera rigida*; Hemimycale columella; Haliclona sp. 4*; Cliona celata*	Scypha ciliatum; Dysidea fragilis*; Stelligera rigida*; Haliclona sp. 4*; Eurypon major*	
Whirlpool Cliff (panels)	Halichondria panacea*; Scypha ciliatum*; Esperiopsis fucorum*; Stelligera rigida; Suberites carnosus	Plakortis simplex; Clathrina coriacea; Aplysilla rosacea; H. brøndstedi; L. complicata	Plakortis simplex; A. rosacea; Clathrina coriacea; Haliclona sp. 7; H. brøndstedi	Halichondria panacea*; Scypha ciliatum; Esperiopsis fucorum; Tethya aurantium; Dysidea fragilis	Halichondria panacea*; Scypha ciliatum; Dysidea fragilis; Hemimycale columella; Esperiopsis fucorum	Scypha ciliatum; Halichondria panacea; Esperiopsis fucorum; Dysidea fragilis; L. complicata	Halichondria panacea*; Scypha ciliatum*; Dysidea fragilis; Stelligera rigida; Haliclona sp. 4

An asterisk indicates that the species is characteristic of the site or habitat to its left; an unasterisked species is characteristic of the site or habitat at the top of the column.
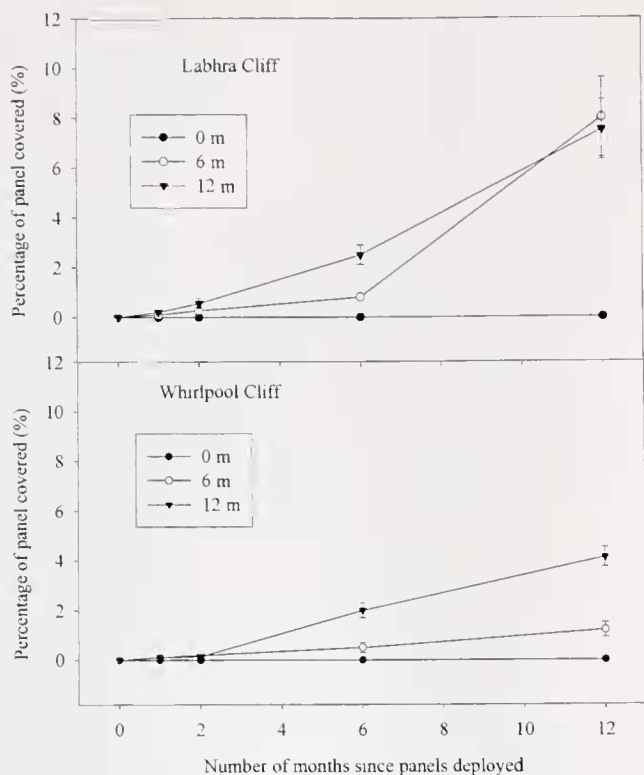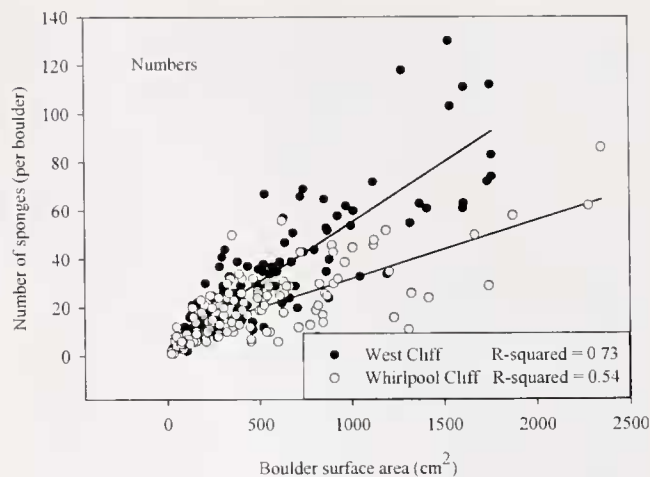
Figure 5. The proportion of artificial settlement panels covered in sponges after 1, 2, 6, and 12 months of deployment at high-energy (Whirlpool Cliff) and low-energy (West Cliff) sites at Lough Hyne.

Figure 7. The linear relationship between sponge densities and rock surface area at high-energy (Whirlpool Cliff) and low-energy (West Cliff) sites on the undersides of rocks at Lough Hyne. Number of sponges (West Cliff) = 60.3 ($\pm$ 35.84) + 14.8 ($\pm$ 0.85) $\times$ surface area. Number of sponges (Whirlpool Cliff) = 47.3 ($\pm$ 46.54) + 22.6 ($\pm$ 1.87) $\times$ surface area.

numerator df = 278). However, when GLM ANOVA was used to compare the linear relationship between sponge numbers and rock surface area, a significant difference was found between the slopes of the relationships at West Cliff

and Whirlpool Cliff (GLM ANOVA: F ratio = 16.16, $P <$ 0.001, denominator df = 1, numerator df = 278). Any unit increase in surface area resulted in a greater increase in sponge density at West Cliff than at Whirlpool Cliff. Also, any given rock size harbored a greater number of sponges at West Cliff than at Whirlpool Cliff.

Discussion

Animal communities are known to vary between large geographic areas (scale of kilometers), but the variability between localized habitats (1 to 100 m) under similar environmental conditions is far less well known. This is true for sponge assemblages: broad distributions have been described by habitat at Lough Hyne (Picton, 1991; van Soest and Weinberg, 1980; van Soest et al., 1981), and recently more detailed studies have added environmental variables to such distributions (Bell and Barnes, 2000b, c). As with most, if not all organisms, environmental factors are critical to the distribution of sponge species. To date, little quantitative information has been provided on localized (where confounding factors are minimized) habitat-associated differences between sponge assemblages in temperate localities.

Morphological variability with habitat stability and environmental characteristics

The studied sponge assemblages (within Lough Hyne) varied considerably between habitats of differing stability (i.e., cliff and boulders) and environmental conditions (i.e., high and low flow), even when habitats were separated by only several meters or less. Sponges inhabiting hard sub-

Figure 6. The relationships between sponge species diversity and richness vs. rock surface area at high-energy (Whirlpool Cliff) and low-energy (West Cliff) sites on the undersides of rocks at Lough Hyne. Species diversity (antilog 10) = 2.09 ($\pm$ 0.15) + 2.09 ($\pm$ 0.04) $\times$ surface area.

stratum have been shown to exhibit considerable morpho-
logical adaptation in response to a variety of factors, includ-
ing flow regime, sedimentation, and substratum type, at
both assemblage (Bell and Barnes, 2000d) and individual
levels (Manconi and Pronzato, 1991; Bell et al., 2002). It
seems, therefore, that morphology alone may account for
some of these differences in assemblage composition be-
tween sites and habitats. The two-dimensional nature of
rock (under-surface) habitats undoubtedly accounts for the
high proportion of encrusting forms because the overt three-
dimensional nature of many other sponge species common
to cliff habitats is inhibited (e.g., arborescent forms). High-
energy cliff sites were dominated by encrusting and massive
forms and showed greater levels of similarity (in assem-
blage composition) to rock habitat assemblages than to
those of low-energy cliffs. However, high proportions of
encrusting and massive morphologies were found in both
cliff and rock habitats, although the species compositions
were very different. Morphology alone cannot account for
all the differences found. Organisms living on the under-
sides of rocks have a number of advantages, including
reduced competition from fast-growing algae found on up-
per rock surfaces, since many sponges are considered slow-
growing (Ayling, 1983), and protection against potentially
harmful UV radiation. Underside rock communities also
experience reduced sediment settlement in areas of low
current flow, reduced effects of desiccation (in the inter-
tidal), and reduced predation from fish and other large
invertebrates (Dunlap and Pawlik, 1996; Wulff, 2000). A
combination of these factors may account for the presence
or absence of any single species on the undersides of loose
rocks. Therefore, the distribution and habitat of each species
should be considered individually.

Morphology alone has already proved valuable in sepa-
rating sponge assemblages inhabiting sublittoral cliffs (Bell
and Barnes, 2000a). Increased numbers of delicate morphol-
ogies, exhibited by a number of species exclusive to low-
energy sites, have been associated with decreasing flow rate
and as a mechanism to reduce sediment settlement (Bell,
2001). However, the rate of water flow had little effect on
the sponge assemblages found on rocks and apparently was
not a regulatory factor of such assemblages (in the present
study). One aspect of morphology that was not considered
within this study is the potential importance of the surface
texture of encrusting sponges in response to habitat distur-
bance or stability. For example, sponges with smooth sur-
faces may be suited to areas of high current flow since they
experience reduced drag. Also, the actual flow (in terms of
speed and direction) experienced by sponges may be sig-
nificantly influenced by seabed characteristics (Hiscock,
1983), such that their morphology and species distribution
may be influenced by microscale environmental character-
istics, which are themselves difficult to characterize. For
example, the overlying nature of loose rocks may lead to
localized areas of negligible current flow, even in high-
current areas.

Assemblage composition variability with flow rate and rock size

Negligible (between-site) differences in sponge diversity
or species richness attributable to flow rate were found on
the under-surfaces of rocks. This suggests that in rock
habitats unlike cliff habitats (Bell and Barnes, 2000a), water
flow rate is not directly important in determining the com-
position of sponge assemblages. Sponge diversity and rich-
ness did, as with most organisms, increase with area (rock
size), which is usually termed an area effect. The density of
sponges for any given rock size was greater at West Cliff
than at Whirlpool Cliff, most likely due to reduced compe-
tition in low-energy environments from superior spatial
competitors such as colonial ascidians and anthozoans
(Maughan and Barnes, 2000b; Bell, 2001a; Bell and Barnes,
2003). Increased sedimentation, to which sponges may
show morphological and physiological adaptation, has been
credited for the shift in competitive ability (Bell, 2001a).
However, since the organisms inhabiting the undersides of
rocks experience little direct sedimentation, other factors
must be responsible for the lack of superior competitors,
such as increased sediment loading (rather than direct set-
tlement) in the water, a condition that sponges appear to
tolerate (Lilly et al., 1953). Also important is the difference
between upper and lower rock surfaces. The domination of
sponges on lower surfaces relates to the absence of mac-
roalgae, which has been considered to control both large-
and small-scale sponge distributions (Witman and Sebens,
1990). Sponge proliferation on upper surfaces may also be
prevented by interference competition from the sweeping
action of algal fronds, as suggested for other invertebrates
(Jenkins et al., 1999). The linear increase in the number of
sponges with increasing surface area of rock may appear
unusual. One might expect that the dominant sponge species
would occupy most of the primary substratum (Russ, 1982;
Maughan and Barnes, 2000b). However, competitive en-
counters and interactions between sponges may be non-
hierarchical and resemble a network (Buss and Jackson,
1979; Bell and Barnes, 2003), thereby preventing monospe-
cies dominance. Even if certain sponge species inhabiting
rocks are dominant over others, these species may show
seasonal growth and retraction of tissue that prevents them
from monopolizing rock surfaces (Sarà, 1970; Stone, 1970;
Elvin, 1976; Barthel, 1989). The distribution of sponges
may also be limited by other biological factors, in particular
predation (e.g., Wulff, 1995); but in the observations of
sponge assemblages at Lough Hyne, predation of sponges
was rarely observed. Fish feeding on algae sometimes broke
branches from arborescent species on cliffs, but extensive
predation was not seen. Sponge population heterogeneity is
also affected by competitive processes (Becerro et al.,

1994), because interactions between spatial competitors influence the direction of growth (in encrusting species) and lead to the patchiness observed within habitats.

Disturbance has been considered an important factor structuring marine epifaunal communities, and rock size has been considered a surrogate of such disturbance (Dayton, 1971; Osman, 1977). This theory is based upon the principle that smaller rocks are more likely to be moved than larger rocks. However, all but the smallest rocks at Lough Hyne showed very similar sponge assemblages across sites experiencing differential flow rates. Sponge assemblages do vary between some surrogate measures of disturbance (flow rate), but not between actual extremes of habitat stability. This suggests that treatment of rock surface area as a surrogate measure of disturbance is unsatisfactory and shows no correlation between extremes of surrogate (*i.e.*, small and large rocks) and true (*i.e.*, high- and low-energy sites) measures of disturbance. At Lough Hyne, small rocks are often held in place by overlying larger rocks, as a result, the probability of motion can be lower (rather than higher) for small rocks than for larger rocks, because the movement of smaller rocks is dependent on the movement of larger rocks *a priori*. Thus, lack of space rather than level of community development (and age) can explain why impoverished sponge assemblages are seen more frequently on small rocks. For organisms (including sponges) that inhabit disturbed habitats (such as loose rocks), succession will be important in structuring the community. Occasional disturbance will prevent the development of a climax community and permit colonization by weaker competitors that might have been excluded from a habitat that had reached a state of climax.

Sponge assemblages on panels had little similarity with other habitats examined and, in contrast to findings with other taxa (Maughan and Barnes, 2000a; Barnes and Maughan, 2001), showed negligible inter-site differences. However, the space occupation (percentage cover) of sponges during the development of the (pioneer succession) panel assemblage varied significantly over the 12-month deployment period (continuous immersion for 12 months). The greater area occupied by sponges on the undersides of panels at Labhra Cliff than Whirlpool Cliff is consistent with the results of other studies of sponge assemblage differences between cliff environments at these two sites (Bell and Barnes, 2000a, d). Sponges are more abundant on panels, rocks, and cliffs at low-energy sites in Lough Hyne than at high-energy sites. Again, this is most likely due to reduced competition in low-energy environments from superior spatial competitors, such as colonial ascidians and anthozoans (Maughan and Barnes, 2000b; Bell, 2001; Bell and Barnes, 2003). All species found on panels submerged for 2-month periods were also found on rocks and cliffs. These early colonizers were important to both mature and immature communities, even though sponges are widely regarded as late colonizers (Dayton, 1971; Maughan, 2000).

Since all species found on panels, which simulated early development of rock communities, were also found in cliff and rock habitats, we suggest that habitat is not as critical in determining species composition at this early stage in development as it is in more mature communities. However, sponge assemblages (rather than species) found on panels did show greater affinities with rock assemblages than with cliffs, which is to be expected given that the panels were used as a surrogate for young rock habitats. Even though a number of sponges were reported from the panels, it is also true that most of the species found in this study did not settle on the panels and thus can still be considered late colonizers of benthic communities. For a complete evaluation of the contribution of sponges to communities of different ages (since panels represent a pioneer succession stage, while cliff communities may be many years old), monitoring must extend over many more time intervals than in the present study. Small rock assemblages had a much greater affinity with the species found to inhabit panels, with two species (*Leucosolenia complicata* and *Scypha ciliatum*) being of particular interest. The presence of these two calcareous species is consistent with other studies of panels (Maughan and Barnes, 2000b) and of the early development of hard-substratum communites (Osman, 1977). These were two of only three calcareous sponges reported during the study, and they appear to be *r*-strategic, or opportunistic, in the use of newly available space. It is unclear if the calcareous nature of these sponges provides them with some adaptive advantage over siliceous sponges.

Are there discriminating species for (local) habitats of differing stability and experiencing different flow rates?

Most habitats and sites could be characterized by several abundant sponge species. Different cliff sites were easily distinguishable from each other and from other habitats on the basis of many species. In rock habitats seven species differed between the high- and low-energy sites, though they were too rare to be between-site discriminating species (as determined by SIMPER analysis). Given the similarities in assemblage composition, it is not surprising that the five most important discriminating species between rock and other habitats did not differ between sites. The low number and ubiquitous nature of species on artificial substrata made the identification of true inter-site discriminating species in this habitat irrelevant.

Are there consistent similarities or differences in assemblage composition from extremes of flow rate and habitat stability?

Although certain environmental characteristics have been found to influence sponge communities, patterns of sponge assemblages on rocks are not consistent with those described from other hard-substratum environments (Storr, 1976; Alvarez *et al.*, 1990; Witman and Sebens, 1990; Bell

and Barnes, 2000a). From our results, the abundance of sponges on rocks, but not the composition of the assemblage, seemed to be manifestly affected by rate of water flow.

Despite the late-colonizer "tag" applied to sponges in marine communities (Dayton, 1971; Maughan 2000), the present study found a number of species contributing to lithophyllic communities on panels that had been deployed for only a few months. Rock habitats did not display a consistent trend of decreasing similarity in assemblage composition from extremes of environmental stability, and rock size was judged to be more important than current flow rate in determining sponge assemblage composition. Disturbance seemed to be more important in determining sponge assemblage composition on cliffs than in loose rock habitats. This study has shown that habitat stability is an important factor to be taken into account along with other measures of disturbance such as flow rate, when considering the distribution of sponge species.

Acknowledgments

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